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A NEW MODE OF SEGREGATION IN GREGORY'S TETRAPLOID PRIMULAS

IN a recent paper¹ Gregory reports a very interesting case in which two different races of *Primulas* suddenly gave rise to giant tetraploid forms, having double the usual number of chromosomes, and apparently having the factors doubled also (individually), for this was true of all the factors which could be followed in his hybridization experiments. It is important to know how segregation will take place in such individuals, as there are four allelomorphs of each gene present.

Let us suppose that a tetraploid form pure for the dominant factor A (and therefore of composition $\frac{A}{A} \frac{A}{A}$) is crossed with a pure recessive giant ($\frac{a}{a} \frac{a}{a}$). Gametes AA and aa will meet in fertilization, forming the hybrid $\frac{A}{a} \frac{A}{a}$ (the maternally derived genes are represented on one line, say the upper, the paternally derived genes on the other line).

Now, if this were an ordinary case of "multiple factors"² in a diploid organism, although the two dominant factors, which we may again call A's, may produce the same effect upon the organism, yet they are not interchangeable, and the same is true of the recessive factors. That is, if we call both dominants A, we must designate one of them as A¹, and the corresponding recessives must also be designated as a and a¹, for A will always segregate into a different gamete from a, and A¹ from a¹, there being two distinct allelomorphic pairs. On the chromosome view of heredity, we would say that A and a always lay opposed to each other, in homologous chromosomes, on the spindle of the reduction division, as did also A¹ and a¹, but neither A nor a lay in chromosomes homologous to those of either A¹ or a¹, and assorted independently of them. The line-up of factors on the spindle in the reduction division in this case would be equally likely to be $\frac{A}{a} \frac{A^1}{a^1}$ or $\frac{A}{a} \frac{a^1}{A^1}$, depending merely upon which

¹ R. P. Gregory, "On the Genetics of Tetraploid Plants in *Primula sinensis*," *Proceedings of the Royal Society*, 1914.

² i. e., a case where two (or more) independent pairs of factors produce similar effects, upon the same character. Many examples of this are known, e. g., the inheritance of red flower in flax.

way the pairs are turned with reference to each other. The first alignment gives gametes AA^1 and aa^1 , the second gives Aa^1 and aA^1 . Thus three gametes with a dominant factor to one pure recessive would on the average be produced, the ratio being $1AA:2Aa:1aa$, omitting primes.

In a tetraploid form, however, A and A^1 are alike and interchangeable, as also are a and a^1 . In the hybrid $\frac{A}{a} \frac{A^1}{a^1}$, therefore, there would be at least one other mode of pairing of allelomorphs possible, giving two new modes of line-up on the reduction spindle, and they would occur just as frequently as the two previous kinds. The two new arrangements would be $\frac{A}{a^1} \frac{A^1}{a}$, giving gametes AA^1 and a^1a , like those in the first of the two previous cases, and $\frac{A}{a^1} \frac{a}{A^1}$, giving gametes Aa and a^1A^1 .³ These latter gametes would be indistinguishable from the Aa^1 and aA^1 gametes given by the second of the two usual arrangements unless A could be distinguished from A^1 and a from a^1 . This could happen only if the allelomorphs were of four different kinds or if there were linkage of these genes with other genes for which the plant was heterozygous. Unless, therefore, linkage or multiple allelomorphism were involved, we could not distinguish between this mode of pairing of allelomorphs and the usual kind; both would give three gametes containing at least one dominant, to one pure recessive (*i. e.*, $1AA:2Aa:1aa$, omitting primes).

Still a third type of pairing of allelomorphs is possible in a tetraploid plant, however. There seems no *a priori* reason, on the chromosome view, why, in a tetraploid plant, a gene should have to segregate from one of the allelomorphs derived from the opposite parent. That is, in a plant of composition $\frac{A}{a} \frac{A^1}{a^1}$, paternally derived genes being indicated on, say, the upper line, maternally derived ones on the lower, there is no apparent reason why the line-up of chromosomes at reduction should not be $\frac{A}{A^1} \frac{a}{a^1}$ or as often as it is one of the other types, since all four chromosomes are homologous. Thus we should get gametes Aa , A^1a^1 , Aa^1 and A^1a .

³ If linkage with other genes could be followed, we should with this mode of pairing obtain crossing over between the chromosomes containing A and a^1 , respectively, and between those containing A^1 and a , respectively; this would not occur on any other mode of pairing.

We could distinguish such gametes individually from those obtained by the ordinary arrangements only if linkage were involved, for then we should sometimes obtain results indicating that the chromosomes containing A and A^1 had crossed over with one another, and so had probably behaved as homologous chromosomes at the reduction division. However, we could also determine whether this mode of pairing occurred or not merely by determining the relative numbers of the different kinds of gametes formed. For, if the third type of pairing occurred, we should obtain $4Aa$ gametes in addition to the $2AA$, $4Aa$ and $2aa$ derived from the other two types of pairing. The ratio of gametes would then be five containing a dominant to one recessive, there being $1AA:4Aa:1aa$, as opposed to the ratio $1AA:2Aa:1aa$ obtainable on either of the other modes of segregation.⁴ The latter or more usual ratio is the only one considered by Gregory, who apparently takes it for granted that in so far segregation must be of the same sort as in diploid forms.

Let us see which ratio is more in accord with his experimental data. As the ratio of offspring in a back-cross is the same as the gametic ratio, it will be seen that a back-cross of $\frac{A}{a} \frac{A}{a}$ by a recessive should give $3A:1a$ plant on Gregory's view, the $3A$'s consisting of $1 \frac{A}{a} \frac{A}{a} : 2 \frac{A}{a} \frac{a}{a}$. On the other view, a back-cross should result in $5A:1a$, the $5A$'s consisting of $1 \frac{A}{a} \frac{A}{a} : 4 \frac{A}{a} \frac{a}{a}$. On inbreeding an $\frac{A}{a} \frac{A}{a}$ plant, however, owing to the random fertilization of gametes, Gregory's $3:1$ gametic ratio would result in a $15:1$ ratio among the offspring (which correspond to F_2) and our own $5:1$ gametic ratio would give a $35:1$ ratio of A to a among the offspring.

A summary of his back-crosses of P_1 heterozygous thrum-eyed plants of the type $\frac{A}{a} \frac{A}{a}$ to recessive pin-eyed plants $\frac{a}{a} \frac{a}{a}$ gives the result 61 thrum:6 pin (10:1, as compared to the two expectations 3:1 and 5:1). Among the F_1 thrums there should

⁴ Counts of chromosomes in the maturation divisions of the tetraploid plants show that the chromosomes synapsed in pairs, not in groups of four. Synapsis in fours would be, in effect, the same as pairing of the random sort suggested in this paper, so far as any one set of allelomorphs are concerned, but it might give different linkage results.

on Gregory's view be $1 \frac{A}{a} \frac{A}{a} : 2 \frac{A}{a} \frac{a}{a}$, on the other view $1 \frac{A}{a} \frac{A}{a} : 4 \frac{A}{a} \frac{a}{a}$. Tests of twenty-one F_1 thrums, by mating them to themselves and also to recessives, showed that there was only one which was certainly $\frac{A}{a} \frac{A}{a}$ and 15 which must have been $\frac{A}{a} \frac{a}{a}$. (A few gave numbers too small to be significant, and one or two were of doubtful composition.) This result is within the limits of probable error on the 4:1, but hardly on the 2:1 expectation. The one F_1 thrum plant which was of composition $\frac{A}{a} \frac{A}{a}$ gave, on back-crossing, 67 thrums:18 pins, a ratio of 3.7:1, to correspond with Gregory's 3:1 or my 5:1 expectation. On inbreeding it gave 44 thrums:2 pins, a ratio of 22:1, to correspond with Gregory's 15:1 or my 35:1 expectation. The other F_1 thrums, being of composition $\frac{A}{a} \frac{a}{a}$ (aside from the few doubtful ones), gave, on the average, 1 thrum:1 pin on back-crossing, and 3 thrums:1 pin on inbreeding; these results would be expected on either view.

Crosses were also made involving the character green versus red stigma (green being dominant). Here the $\frac{A}{a} \frac{A}{a}$ forms, on back-crossing, gave a total of 114 green:30 red (3.8:1 instead of 3:1 or 5:1), and on inbreeding they gave 75 green:2 red (37.5:1 instead of 15:1, as on Gregory's expectation, or 35:1, on my own).

It will be seen that the numbers in the above crosses are too small to be very significant, individually, for a settlement of the question at issue, but if summed up they become more decisive. Thus, a summary of the offspring of all back-crosses of the $\frac{A}{a} \frac{A}{a}$ form to the recessive gives 242 dominants (A):54 recessives (a), or 4.5:1, as compared with the 3:1 expectation of Gregory and the 5:1 of the view advocated in this paper. Where the dominants among these offspring were tested they were found to consist of $1 \frac{A}{a} \frac{a}{a}$ and $15 \frac{A}{a} \frac{A}{a}$, as compared with the 1:2 expectation of Gregory, and ours of 1:4. Finally, a summary of the cases where $\frac{A}{a} \frac{A}{a}$ forms were inbred shows that 119 dominants:4 recessives resulted, a ratio of 30:1 where Greg-

ory's expectation would be 15:1 and our own 35:1. Moreover, the individual records fluctuate in both directions about the ratios to be expected upon our point of view, but practically all vary in the same direction from the expectation of Gregory, namely, in the direction of the other expectation.

There is reason, then, to believe that in these *Primulas* the factors derived from the same parents may segregate from each other as allelomorphs, while allelomorphs derived from opposite parents meanwhile assort at random. For although the allelomorphs exist in sets of four they must pair two by two for segregation, as do the chromosomes, and two derived from the same parent may happen to pair with one another. The chance that this should occur is one third, since there are three possible modes of pairing. Such a result is difficult to explain except on the chromosome view of heredity. It would give ratios different from those theoretically expected by Gregory, but more in accord with his experimental data. The principle upon which our own expectation is founded may be briefly summed up by saying that where more than two factors which are normally allelomorphous to each other are present, the pairing of these allelomorphs with each other preparatory to segregation usually⁵ takes place at random.

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⁵ That this is not always true is shown by Bridges' case of "non-dis-junctional" females of *Drosophila*, which contain one Y and two X chromosomes. Any two of these chromosomes normally act as homologues to each other in the reduction division of the normal fly, which contains only two of them. But where all three are present together they do not pair at random, for they oftener undergo the segregation X-XY than XX-Y, presumably because the two X's are much more like each other than like the Y, and so more apt to act as homologues.